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RESEARCH PAPER

Floristic patterns in the Andes of northern Patagonia's forests, Argentina: towards integrating ecological responses with expert-based and unsupervised classification methods

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Abstract

Aims: To explore the relationship between plant communities and key environmental drivers in the Andes of northwest Patagonia, Argentina, and to evaluate the applicability of traditional phytosociological definitions to this region. **Methods:** We conducted 141 vegetation samples using a stratified systematic sampling design. This was done along two steep gradients of aridity and temperature, which are further modified by local factors that include successional changes due to fire and soil variation. We employed a series of multivariate approaches, including hierarchical clustering, Indicator Species Analysis (ISA), restricted Monte Carlo permutation tests, and both constrained and unconstrained ordinations, to identify (a) the main plant community types, (b) their representative species, and (c) the primary drivers of variation in species composition. Finally, we compared the obtained groups and species to associations described by earlier expert-based classifications. **Results:** From the set of analyses, we identified six different plant community types with 241 recorded species. We found significant differences across communities' species composition and their environmental indicators. Among the considered environmental variables, elevation and annual precipitation had the strongest effect on species composition. Additionally, variation in composition was significantly related to forest structure, land use and soil characteristics. We further outlined the influence of locally biased classifications based on a predominance of sampling in areas western to the Andes in classification systems developed in the region. **Conclusion:** Our analysis allowed us to identify the most relevant environmental drivers and indicator species of the six classified plant communities based on numerical methods. The findings highlight the importance of considering full ecological gradients and communities' responses for developing stable classification approaches.

Taxonomic reference: Anton and Zuloaga (2023).

Abbreviations: db-RDA = distance-based Redundancy Analysis; ISA = Indicator Species Analysis; NMDS = Non-metric Multi-Dimensional Scaling.

Keywords

Climate gradients, forest vegetation, indicator species, Patagonia, plant communities, unsupervised classification

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Introduction

The species composition of a region forms an ecological mosaic largely shaped by environmental variation (Whittaker 1956; Tuomisto et al. 1995). In the field of vegetation ecology, communities are influenced by a complex interplay of structuring factors (Dray et al. 2012), including both top-down (macro-scale) and bottom-up (micro-scale) controls (*sensu* Whittaker et al. 2001). Research has consistently demonstrated that variation in species composition is explained by a range of drivers at different scales, such as climate (Whittaker 1956; Myers et al. 2013), relief or topography (Legendre et al. 2009), soil characteristics (Speziale et al. 2010), human impact (Piazza et al. 2016; Khan et al. 2019), and habitat structure (Chillo et al. 2020; Majeed et al. 2022; Rodríguez and Soler 2023). In temperate forests, this dynamic is particularly evident, as species aggregation tightly correlates with environmental conditions, emphasizing the role of species-sorting mechanisms like environmental filtering (Myers et al. 2013). In a current scenario where the growth conditions and disturbance regimes of temperate forests are undergoing rapid change, the study of these interactions becomes even more urgent (Kelly and Goulden 2008; Adler et al. 2022).

Understanding vegetation responses to the environment is essential for building consistent classification approaches (De Cáceres et al. 2015). This understanding is vital for conservation planning and ecosystem management as it enables anticipation of climate impacts on vegetation and the development of proactive strategies. (Myers et al. 2000; Dray et al. 2012). Additionally, clarifying the relationship between environmental factors and vegetation patterns improves the use of species as indicators of soil properties (e.g., pH, moisture, salinity), disturbances and bioclimatic conditions (Ellenberg et al. 2001; Amigo and Rodríguez-Guitián 2011; Huertas Herrera et al. 2018). Studying understory species introduces another layer of complexity, where the overstory influences the forest microclimate, the biogeochemical cycle in the soil (litter, humus layers and rhizosphere), and light availability on the forest floor, thereby affecting habitat suitability for understory species (Alonso et al. 2020; Chillo et al. 2020). Exploring these relationships across different forest ecosystems and scales informs adaptive management strategies (Dray et al. 2012; Page and Shanker 2018).

The Andes of northern Patagonia are characterized by pronounced moisture and elevation gradients, providing a unique opportunity to study the effects of climatic gradients on vegetation (Paruelo et al. 1998; Kitzberger et al. 2022). The region exhibits a clear two-dimensional zonation of vegetation. The longitudinal zonation is characterized by a strong rain-shadow gradient, ranging from broadleaved wet forests rich in hygrophilous species in the west to mesic mixed forests and dry conifer forests in a sub-Mediterranean climate in the east. The elevation zonation is characterized by a belt of evergreen mixed forests of *Nothofagus dombeyi* and *Austrocedrus chilensis* from lower to mid-elevations. The sub-Andean (hereafter: "subandean") belt is dominated by high-elevation woodlands of *Nothofagus pumilio*, appearing in a broad variety of growth forms, reaching from tall deciduous forests to dwarf scrubs near the timberline (Eskuche 1973, 1999; Cabrera 1976; Amigo and Rodríguez-Guitián 2011). Moreover, the Patagonian Andes region is recognized as a biogeographical island, evolving in isolation since the Neogene with endemism rates as high as 50% at the species level (Marticorena 1991; Arroyo et al. 2008).

Research in this region has examined plant formations across broad spatial scales (Luebert and Pliscoff 2006; Amigo and Rodríguez-Guitián 2011), exploring their correlations with bioclimatic belts using global classifications developed by Rivas-Martínez et al. (2011). Further ecological studies have focused on the dominant species and their characteristics (Veblen et al. 1996; Donoso Zegers 2006) and the impact of herbivory by large introduced mammals (Relva and Veblen 1998; Veblen et al. 2011). Forest fire dynamics have been extensively studied as a key driver of vegetation changes (Veblen et al. 1999; Kitzberger 2012), resulting in large post-fire succession areas dominated by deciduous shrublands of *Nothofagus antarctica*. Despite significant advancements in understanding the vegetation ecology of the Patagonian Andes, research on community-level responses remains scarce but essential (Soler et al. 2019; Chillo et al. 2020). Additionally, challenges in achieving consensus on classification systems underscore the need for further research and collaboration in this field.

Oberdorfer's contributions in 1960 provided the basic lattice for a floristic classification system. His studies in Chilean northern Patagonia identified biogeographical origins as the primary factor defining two contrasting classes which are (1) the *Wintero-Nothofagetea* Oberd. 1960 evergreen montane forests and (2) the *Nothofagetea pumilionis-antarcticae* Oberd. 1960 deciduous forests (Oberdorfer 1960). Later in Argentina, Eskuche (2002, 1999, 1973, 1968) and Seibert (1979) placed the majority of their surveys in the *N. dombeyi* evergreen forests within the class *Nothofagetea pumilionis-antarticae* considering a new set of indicator species comparing to the original class defined by Oberdorfer in 1960. Eskuche names a few exceptions of forests in the west of Argentina classified under *Wintero-Nothofagetea*, but states this class is mostly present West to the Andes in Chile. He proposes a new alliance, *Nothofagion dombeyi* Esk. 1999, to include these *Nothofagus* forests along with *Austrocedrus chilensis* forests as the main tree species. This reclassification to the class *Nothofagetea pumilionis-antarcticae* aims to better reflect the consistent occurrence of characteristic species at the alliance, order, and class levels.

Interestingly, while most subsequent studies cite the associations proposed by Eskuche, they do not adopt his class reclassification. The narrative definitely diverges with the analysis provided by Pollmann (2001), which takes different sources covering a greater geographical extent and defines diagnostic species down to the alliance level, placing all *N. dombeyi* forests in the *Wintero-Nothofagetea*

class. Pollmann defends that the order *Berberberido trigonae-Nothofagetalia dombeyi* Pollmann 2001 should be in the Valdivian class, since it lacks the high mountain species that differentiate the class of the subandean forests. However, Argentinian surveys are underrepresented in Pollmann's tables and leave out *Nothofagus antarctica* montane shrublands. Moreover, the alliances consist of associations of which diagnostic species were defined by Eskuche in Argentina and rarely match those proposed by Pollmann at the alliance level. Another key source, *Transecta Botánica Austral*, one of the most comprehensive geobotanical studies covering the full precipitation gradient from Chile to the Atlantic coast in southern Patagonia, highlights shrublands as transitional stages of deciduous forests, aligning with Oberdorfer's initial 1960 classification (Boelcke et al. 1985). Finally. reviews by Amigo and Rodríguez-Guitián (2011, 2015) bring further insight and provide a home for *Nothofagus antarctica* montane shrublands as a seral stage in the *Wintero-Nothofagetea* class and shrublands developed in the orotemperate belt such as *Krummholz* into *Nothofagetea pumilionis-antarcticae.* In a recent study, authors suggested classifying the fringe vegetation of the *Wintero-Nothofagetea* forests as a new class, *Aristotelietea chilensis* Amigo et al. 2022 (Amigo et al. 2022). Communities dominated by *Nothofagus antarctica*, like *Lomatio hirsutae-Nothofagetum antarcticae* Esk. 1969 in the meso-supratemperate zones, align well with this classification, fitting into a *Nothofago antarcticae-Berberidion darwinii* Esk. 1969 alliance within the *Aristotelietea chilensis* class.

Nevertheless, except for Eskuche's surveys, all the mentioned studies were carried out in northern Chilean Patagonia without considering the more arid extreme of the rain-shadow gradient. Additionally, early studies were limited by non-systematic sampling methods, a lack of reproducible numerical analyses, and inconsistent terminologies and classifications, underscoring the need for a more formal approach to studying the region's vegetation. Our study builds on previous research efforts, including broader-scale classifications, and adopts a systematic and exploratory approach, utilizing geo-referenced sampling and advanced numerical analyses to reveal the floristic patterns of the Rio Puelo watershed in north-west Patagonia. We investigate how a comprehensive set of factors, namely climate, topography, soil characteristics, forest structure, and human activities contribute to variation in species composition. We subsequently identify plausible plant communities within the study area; determine their distinct species compositions and the biotic and abiotic factors that define these groups. Finally, we analyze how the classified plant communities and their ecological response align with expert-based traditional classification systems and assess if the membership rules and diagnostic species predominantly developed in Chilean forests and coarser scales are practicable at a finer sub-regional scale in Argentina. This approach ultimately contributes to refining and validating these syntaxonomic classifications for use in environmentally diverse, fine-scale contexts.

Materials and methods

Study area

The Rio Puelo catchment area spans between 41.2° to 42.5° South and 72.2° to 71.5° (Figure 1). The region exhibits a steep hydrometeorological gradient due to the rain-shadow effect of the Andes, where precipitation and productivity decrease from the Chilean Andes in the west to the steppe boundary in the east. Additionally, an elevation gradient is marked by a linear decrease in temperature with elevation, alongside increasing rainfall and snowfall. The interplay of Pacific and Atlantic high pressure centers, the sub-polar low-pressure belt, and their fluctuations, drive strong precipitation seasonality and interannual variability (Paruelo et al. 1998; Lara et al. 1999). Biogeographically, the region has been defined as the sub-Andean Province, between the wet Valdivian Province in the west and the dry Central Patagonian Province in the east (Morrone 2001), the sub-Antarctic province (Cabrera 1976) and Valdivian-Magallanic region (Rivas-Martínez et al. 2011). In this region, the north Patagonian- sub-Antarctic laurophyllous and coniferous mixed forests and sub-Antarctic Andean deciduous forests are close to the dry and / or warm climatic edge of their distribution (Amigo and Rodríguez-Guitián 2011).

Summer fires are frequent in Patagonia and three major fires have occurred within the study area in recent decades: "El Boquete" and "Golondrinas" in March 2021, and "Lago Steffen" in 2023 (Ministerio de Ambiente y Desarrollo Sostenible 2021). However, we verified that the sampled areas remained unaffected by these or any other fires in recent decades (Suppl. material 1).

Sampling design

We combined a purposive sampling with stratification along the precipitation gradient and a systematic sampling along elevational gradients and slope aspects This methodology was employed to capture environmental heterogeneity and facilitate a comprehensive representation of the forest ecosystem within the specified gradients. We defined two transects oriented west-east to align with the precipitation and plant biogeographical gradient, selecting accessible areas.

Within each transect, four distinct sectors were established to represent various moisture conditions across the precipitation gradient. Each sector divided into north and south slope aspects to account for differences in irradiance and wind exposure. Nested within these divisions were elevation sub-transects spanning 500 to 1,600 m a.s.l., featuring 100 m^2 squared plots at every 100 m elevation interval. Soil and forest structure variables were sampled along the elevation-gradient transects of the vegetation relevés (66 sites) together with the forest structure measurements at elevation steps of 200 m (Loguercio et al. 2024). Other soil plots (46 sites) were obtained from

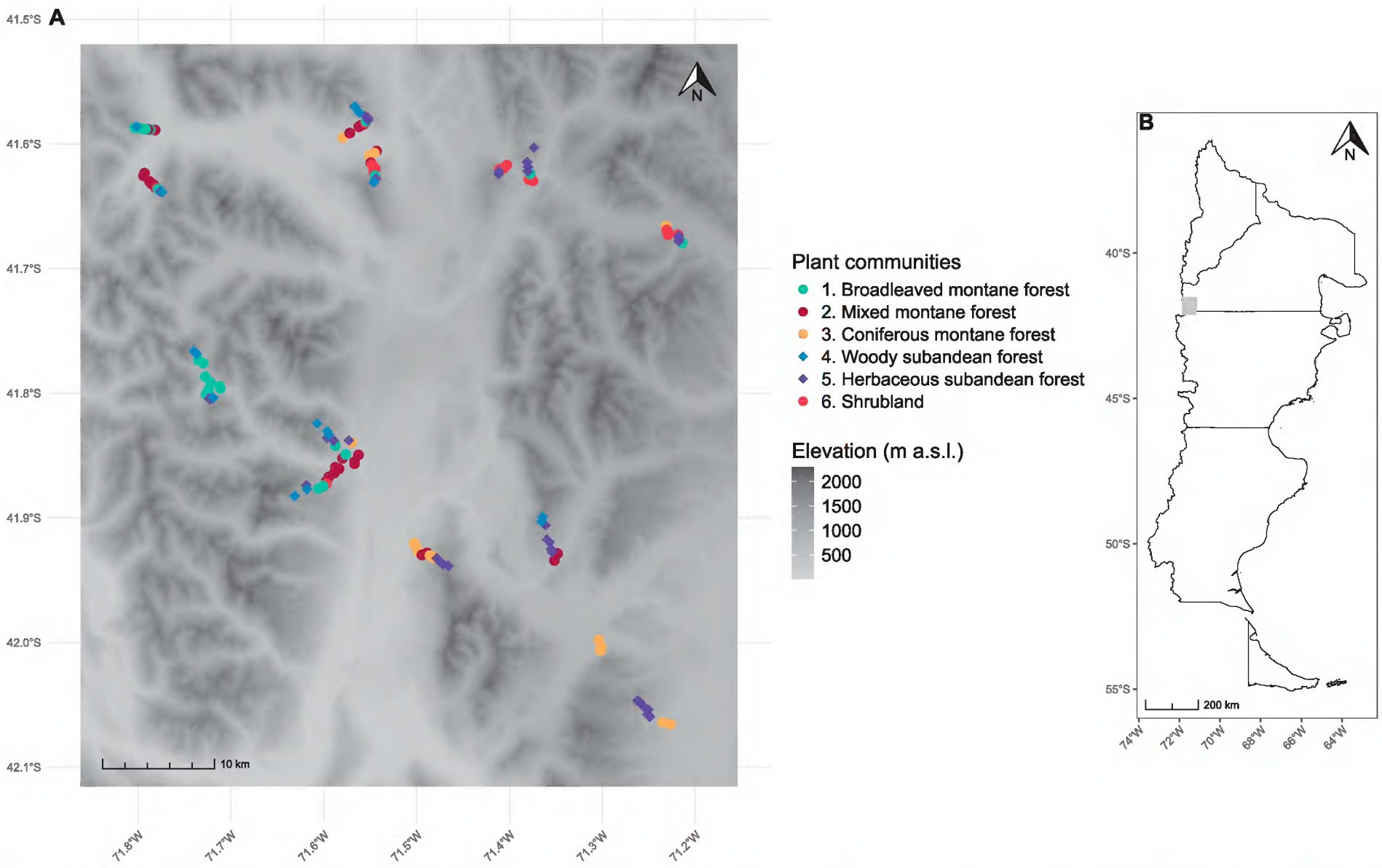

Figure 1. (**A**) Study area depicting sampling plots, color- and shape-coded by vegetation type. The background map shows the elevation gradient from a digital elevation model from the NASA Shuttle Radar Topography Mission (2013) at 30 m resolution (**B**) Map of the Patagonian provinces with the study area located between Rio Negro and Chubut.

a soil survey (Simon et al., unpubl.) to characterize the edaphic heterogeneity in the study area. These plots are located both overlapping or within some distance to the vegetation plots.

Data collection

During the growing seasons from December 2021 to March 2022 and December 2022 to March 2023, we conducted 141 vegetation relevés. Within each plot, species abundance was estimated as percent coverage (1 m^2 = 1%). Additionally, the number of tree stumps and the extent of browsing damage to the plants were recorded (See Suppl. materials 2, 3 for detailed methods). Geographic position and elevation were recorded using a GPS device (Garmin GPSMAP 64s, ± 15 m). We derived elevation and Heat Load Index (HLI) as a measure of the influence of solar radiation (McCune and Keon 2002) from a digital elevation model from the NASA Shuttle Radar Topography Mission (2013) at 30 m resolution and extracted mean annual temperature (MAT) and annual precipitation (AP) from the global WorldClim model (Fick and Hijmans 2017). We used the packages "elevatR" for accessing the digital elevation model (Hollister et al. 2023), "terra" (Hijmans 2024) for working with raster data and "spatialEco" (Evans and Murphy 2023) for computing the Heat Load Index. Maps were developed using QGIS 3.34.3 Geographic Information System (QGIS Development Team 2024).

We investigated the recent fire history of the area using Landsat 5 and 8 TM/ ETM+ at 30 m resolution satellite imagery spanning 1984 to 2023. Satellite image processing was conducted using Google Earth Engine (Gorelick et al. 2017), which applied cloud-masking algorithms to generate cloud-free composites. To assess fire impact, we created burn severity maps using the differenced Normalized Burn Ratio (dNBR). This metric was calculated by subtracting the post-fire NBR (calculated from near-infrared and shortwave-infrared reflectance) from the pre-fire NBR. Burn severity was classified based on thresholds established by the United States Geological Survey (USGS). Areas with a dNBR value greater than 0.44 were categorized as moderate to high severity and deemed "burned" (Miller and Thode 2007; Escuin et al. 2008).

We resolved nomenclatural updates and defined species life form and origin (native, endemic, non-native or cosmopolitan) according to the digital database "Catálogo del Cono Sur" (Anton and Zuloaga 2023), obtaining species lists with the packages "taxlist" (Alvarez and Luebert 2018) and "kewr" (Walker 2021). In the mentioned database, endemic species are defined with reference to the southern cone of South America, which includes Argentina, Chile, Uruguay, Paraguay, and southern Brazil.

In order to characterize the biometric parameters of the forest, we established two concentric circular forest inventory plots at the same location as the vegetation plots. These forest inventory plots were larger in size compared to the 100 m^2 vegetation plots. In a smaller forest invento-

ry plot of 400 m^2 size, we recorded the diameter at breast height (DBH) of all trees—both living and dead—with a DBH ≥ 7 cm. In a larger forest inventory plot of 1,000 m^2, all trees with a DBH > 60 cm were surveyed. We determined the species of all trees in each plot. The mean age of the dominant trees (hereafter, "stand age") was assessed by selecting, in each plot, the proportion of the 100 trees/ha with the largest DBH (Assmann 1970). For this purpose, we extracted two wood cores at breast height, positioned perpendicular to each other and at a 45° angle relative to the axis of the largest diameter.

The humus layer and the mineral topsoil were sampled at locations without topsoil disturbance. The ect-organic humus layer—excluding fresh litter—was completely sampled within a 20 cm × 20 cm frame. For the mineral soil, we used samples from the 0–10 cm depth interval. The soil organic carbon (SOC) concentrations were determined for both, humus and mineral soil samples by ignition at approximately 500 °C (Davies 1974; FAO 2006). The total nitrogen (N) content of both samples was analysed using the semimicro Kjeldahl method (Bremner 1960). From this, we calculated the C/N ratio as an indicator for soil biological activity and nitrogen availability to the plants. The pH of the mineral soil was determined in soil suspended in water at a ratio of 1:2.5, following SAMLA (2004).

Data analysis

Data pre-processing

We compiled a dataset with 13 environmental and stand structural predictor variables, listed in Suppl. material 2. We used slope and elevation derived from the DEM (Suppl. material 2) as predictor variables. We performed a nearest neighbor assignment (QGIS Development Team 2024) to match soil and forest structure data to the vegetation plots where the measurements did not exactly overlap, within a maximum distance of 300 m. This process resulted in a total of 84 vegetation plots with both soil and forest structure data, covering the entire elevation gradient as well as transects and expositions approximately equally to the full dataset.

The following biometric parameters were calculated for each forest inventory plot: stem density [number of trees*ha^{-1}] and cumulative basal area [m^2 per ha^{-1}]. In addition, for each vegetation type, the basal area contribution of each tree species was determined, indicating the mean and its variation (standard error). We estimated a browsing index after Gadola and Stierlin (1978) (see Zerbe et al. 2023; Suppl. material 3: table S.3.1) based on the recorded browsing damage and representing predominantly grazing by cattle. We estimated logging intensity from the number of stumps (Zerbe et al. 2023; Suppl. material 3: table S.3.2).

We applied a logarithmic transformation to the species' percent cover to mitigate the impact of highly abundant species (Tichý et al. 2020). For the ordinations, we excluded the vegetation layer associated with the tree canopy, as our primary focus was on studying its effect (e.g., stand age and basal area as independent predictor variables) on the understory patterns. The 'dplyr' Rpackage was used for data manipulation (Wickham et al. 2023).

Vegetation classification

Since there is a lack of consensus in the phytosociological classification in the Argentinian region, we first identified types using a numerical unsupervised classification. To determine an appropriate cutting level, we visually identified long horizontal lines before steep increases on the fusion level graph (which represents the height dissimilarity values at which dendrogram branches merge), prioritizing groups with a substantial number of sites (Suppl. material 4; Borcard et al. 2018). To optimize for a high number of indicator species, a total of two to ten potential vegetation groups were tested by iterative clustering (Suppl. material 4: figure S.4.1). For this, numbers and mean p-values of significant indicator plant species for the considered potential vegetation groups were observed following Khan et al. (2019).

We employed a Sequential Agglomerative Hierarchical Non-overlapping classification approach using Ward's method, which is based on minimizing the total error sum of squares. Based on the criteria described above, we have set the number of groups to six. Ward´s clustering algorithm was applied to Bray-Curtis distances with a square root transformation to make them metric. We assessed association between the original dissimilarity matrix and the cophenetic distance with a Pearson correlation coefficient. We carried out an Indicator Species Analysis (ISA) of the identified vegetation units following Chytrý and Tichý (2003) with 999 permutations using the 'indicspecies' package (De Cáceres and Legendre 2009). We defined indicator species for combinations of up to three clusters following De Cáceres et al. (2010). For a systematic comparison, we secondly assigned the types to existing associations of the traditional expert-based classification. We based our assignment in the following membership rules: similar physiognomy and dominant life forms, bioclimatic diagnosis, and floristic composition (Figure 2). We compared the data obtained in our vegetation survey and ISA with available literature (Eskuche 1999; Pollmann 2001). We used diagnostic species specified at the alliance level (maximum level of diagnosis achieved by Pollmann 2001 and association level proposed by Eskuche 1999 and (Amigo and Rodríguez-Guitián 2011, 2015); see Suppl. material 5).

Bioclimatic and environmental indicators and diversity analysis

The bioclimates of the types were calculated using the Worldwide Bioclimatic Classification System (WBCS) by Rivas-Martínez et al. (2011), which incorporates moisture and temperature conditions to define bioclimatic classes. Moisture levels were categorized into ombric types based on the ombrothermic index (Io), with classifications such as Hyperhumid and Humid, further divided into 'lower' and 'upper' horizons. Temperature conditions were classified using the annual positive temperature (Tp) as a thermotypic index, with categories like Supratemperate

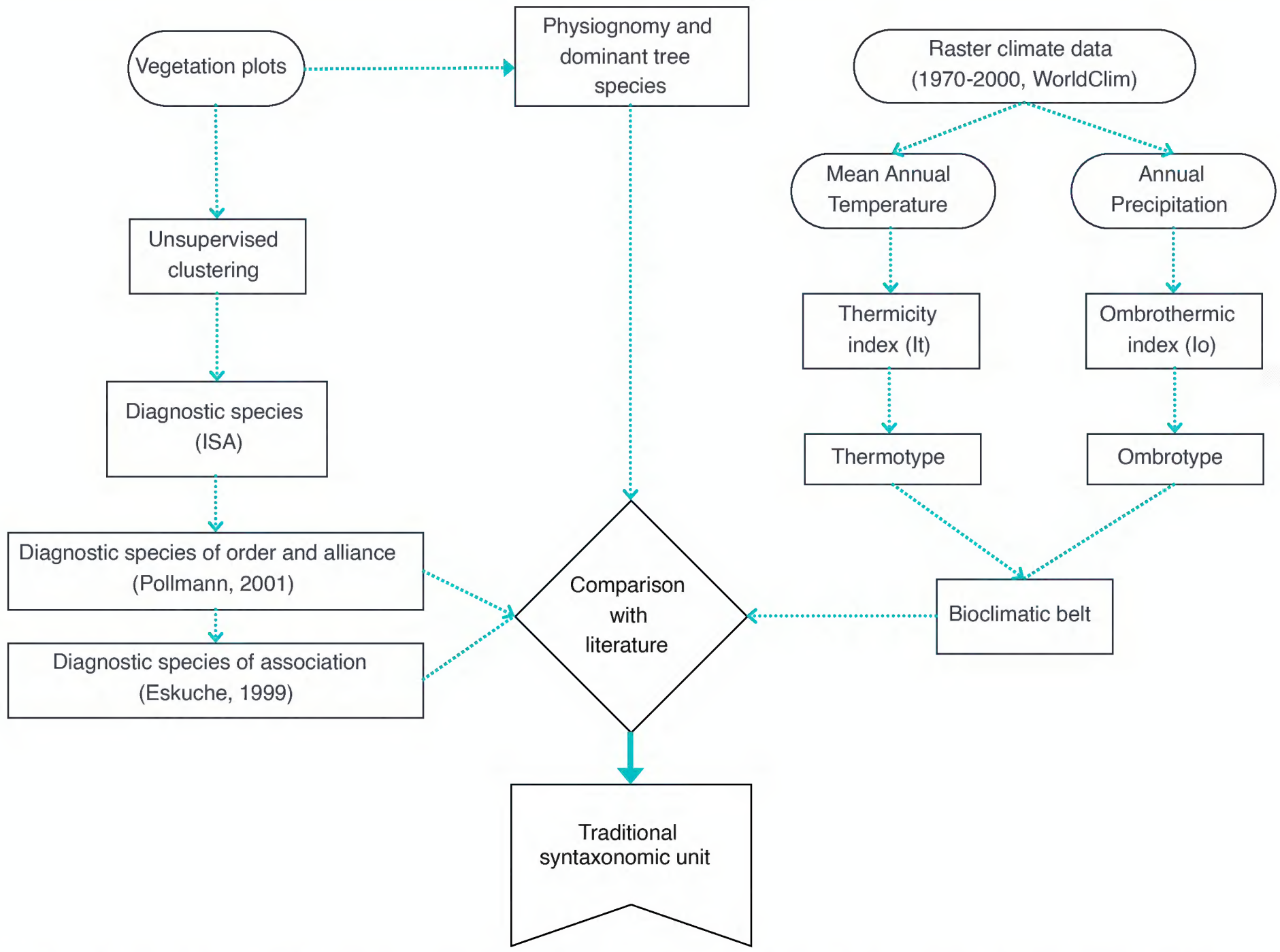

Figure 2. Flowchart of the step-by-step methods and the sources of information applied to compare and assign clusters obtained from the numerical classification to existing traditional associations. The species employed in the assignment are detailed in Suppl. material 5.

and Orotemperate, also split into 'lower' and 'upper' horizons. Since altitude affects thermic variations, we based the macrobioclimate classification (Temperate) on valley floor temperature and precipitation values from the nearest weather station (El Bolsón; 41.96°S, 71.53°W at 345 m.a.s.l.; SMN 2023) with recorded data from 1991 to 2020, following Rivas-Martínez et al. (2011). Although this station represents a lower and warmer area than most surveyed forests, its climate can be classified as Temperate with a sub-Mediterranean variant according to Rivas-Martínez et al. (2011). To remain consistent with classic literature (e.g., Cabrera 1976; Keith et al. 2020), we classified the macrobioclimate as Temperate. For detailed calculations, see Suppl. material 6.

To compare differences in mean soil characteristics across the vegetation types, we conducted a Welch's ANOVA followed by Games-Howell post-hoc analysis for pH, both of which do not require equal variances among groups. We conducted a Kruskal-Wallis test followed by a Dunn's test with Holm's correction to the p-values to analyze the C/N ratio, without assuming a normal distribution. Model assumptions were checked visually. We calculated for each vegetation type mean species richness, Hill-Shannon diversity (Roswell et al. 2021) and Pielou's evenness (Pielou 1975) with the 'vegan' package (Oksanen et al. 2024).

Ordination analyses

To identify main environmental drivers of species compositional change and their relative importance, we performed a constrained ordination analysis, namely partial distance-based redundancy analysis (db-RDA, McArdle and Anderson 2001) based on Bray-Curtis dissimilarities with Lingoes correction (Legendre and Anderson 1999). To avoid confounding effects of the sampling design and to isolate the effect of explanatory variables on species composition, the effect of the transects was partialled out by using it as a conditioning variable. This analysis was performed using the above-described subset of 84 sites.

The strongly positively skewed variables stem density and stand age were log and square-root-transformed, respectively, prior to using them in the analyses. To avoid collinearity issues, a cut-off level of < 0.6 was chosen for the absolute value of Pearson correlation coefficients between potential predictor variables (Dormann et al. 2013). Possible associations between categorical variables were tested by Fisher's exact test. Within these restrictions, we chose a set of nine ecologically meaningful variables for the analysis: elevation, slope, HLI, AP, basal area, stand age, C/N ratio, and pH of the mineral topsoil as well as browsing index.

First, a global model that included all nine variables was built and tested for its significance. Then, a stepwise bi-directional selection procedure was used to identify the environmental variables that had the highest association to species composition. For the final model, including only variables selected by stepwise selection, we tested the marginal significance of the constraining variables with ANOVA-like permutation tests using 9999 permutations. Permutation tests were stratified within transects. For the stepwise selection, p-values were adjusted for multiple testing by Holm's correction (Holm 1979).

To further describe the identified vegetation units, to visualize differences in species composition, and to explore their relationships to environmental variables, we conducted a complementary unconstrained ordination analysis for the entire dataset of 141 sites. We applied non-metric multidimensional scaling (NMDS; Kruskal 1964a, 1964b) based on Bray-Curtis dissimilarities, assessing the quality of different NMDS solutions based on the stress value. The most favorable results, with stress values below 0.2 (Clarke 1993), were achieved when utilizing three NMDS axes. All the explanatory variables of the constrained ordination, as well as supplementary variables for improved interpretability (no. of species and no. of non-native species), were fitted post-hoc on the ordination diagrams using multiple regression. Significance of fitted variables was assessed by 9999 permutations of environmental variables, which were stratified within transects. Species scores were added as weighted averages. Multivariate analyses were performed with the 'vegan' package (Oksanen et al. 2024). Graphs were created using the 'ggplot2' (Wickham 2016), and the 'dendextend' (Galili 2015) packages.

All statistical analyses were carried out using R version 4.2.3 (R Core Team 2023).

Results

Flora of the forests

We identified 230 vascular plant species at the species level and 9 at the genus level, distributed across 70 families and 153 genera (species list in Suppl. material 7). Two species were not identified. The life forms observed included 16 tree species, 10 species categorized as shrubs or small trees, 54 shrub species, 121 perennial herbs, 30 annual herbs, three climbers, four parasites, and one vine. Among these, endemic and native species accounted for 63.6% and 20% of the total, respectively. Non-native species made up 16.38% of the dataset, predominantly consisting of herbaceous life forms (Suppl. material 8).

Effects of environmental variables

Constrained ordination (db-RDA) revealed a significant influence of the tested environmental variables on species composition (global model with nine variables, $p < 0.001$). The stepwise selection procedure identified eight variables: elevation, annual precipitation (AP), browsing index, stand age, basal area, Heat Load Index (HLI) and pH and C/N ratio of the mineral layer. All variables except C/N ratio remained significant ($p < 0.05$) after adjusting for multiple comparisons using Holm's correction, with HLI showing a marginally significant influence ($p = 0.067$).

The final model using the six significant factors explained 26.3% of the variation in community composition with a conditional effect of the transect of 2.6% (total inertia: 45.34, sum of all canonical eigenvalues: 11.95, sum of conditional eigenvalues: 1.14). Elevation had the strongest effect ($pseudoF_{1,74} = 5.63$, $p < 0.001$), followed by AP ($pseudoF_{1,74} = 2.50$, $p < 0.001$) and stand age ($pseudoF_{1,74} = 2.17$, $p = 0.003$). For comprehensive results of the db-RDA, refer to Suppl. material 9: table S.9.1.

Classification of plant communities

When running the cluster analysis with two to ten potential groups, the number of significant indicator species varied between 78 and 130, with their mean p-values between 0.015 and 0.012 (with 999 permutations). The highest number of significant indicator species (130) and lowest mean p-value of 0.011 indicated six ecologically meaningful vegetation groups in the study area (Suppl. material 4). We present the clustering pattern and distance between communities in a dendrogram (Figure 3). The six plant communities were named according to their elevation belt and vegetation features (Suppl. materials 10, 11). Tables detailing the full floristic composition of each vegetation type can be found in the Suppl. material 12 (montane forests), 13 (subandean forests) and 14 (shrublands). We also provide photographs of the classified vegetation units (Figure 4).

Characterization of plant communities

Bioclimatic and floristic diagnosis

The bioclimatic indices computed in this study align well with the zonation observed in the NMDS analysis. The montane are characterized by thermotypic horizons ranging from Upper Supratemperate to Lower Orotemperate, while the subandean communities are situated in the Upper Orotemperate horizon. Elevation was highly negatively correlated to MAT ($r = -0.94$). The ombrothermic index (Io) effectively illustrates a precipitation gradient among the communities, categorizing them from Upper Hyperhumid conditions (montane forests) to Lower Hyperhumid (mixed montane and subandean forests) and Humid conditions (coniferous forests), as detailed in Suppl. material 10: table S.10.1.

Broadleaved montane forest (*Myrceugenio-Nothofagetum dombeyi*). This community was located in the wet areas of our study's western region, adjacent to the Valdivian temperate rainforest. The proximity to the rainforest allow for presence of rainforest species, indicative of moisture

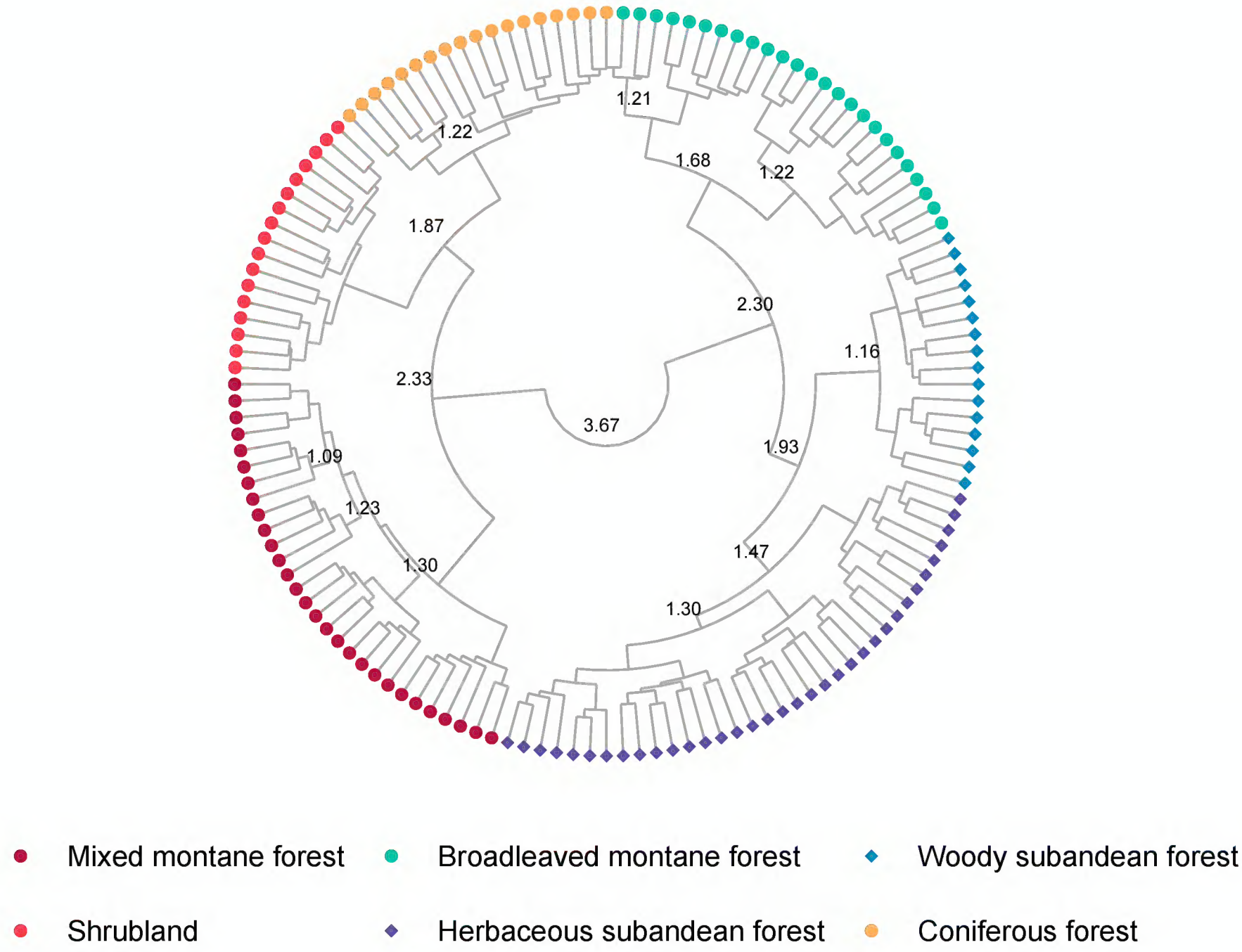

Figure 3. Dendrogram illustrating the clustering pattern of the six plant communities based on squared-root transformed Bray-Curtis distances with cophenetic correlation 0.69. The values on the branches represent the height at which clusters merge, indicating the degree of dissimilarity between clusters. Subandean and montane forests are depicted with different shapes.

and shade tolerance. The community spans an elevation range of 700 to 1200 m a.s.l and experiences a MAT of 6.7 ± 0.86 °C and AP of 1327 ± 140 mm. Analyzed across 26 plots, the average species richness is 14.07 ± 5.06, and Pielou's evenness is 0.64 ± 0.19, this community was the least rich and most even among the montane communities (Figure 6). The indicator species with the highest fidelity coefficients for this community include *Drimys andina*, *Desfontainia spinosa*, *Saxegothea conspicua* and *Berberis trigona* (Table 1). Other ten indicator species were also present in a lesser extent in the mixed montane forests, include the dominant *Nothofagus dombeyi*. This community shares the highest number of species with the subandean forests, as the more humid areas feature a wider ecotone of mixed forests dominated by *N. dombeyi* and *N. pumilio* along the elevation gradient (see Table 1).

Mixed montane forest (*Austrocedro-Nothofagetum dombeyi*). This plant community was identified in the western and transitional zones, with 29 samples (Table 1). It was found at elevations ranging approximately from 500 to 1300 m a.s.l. The community experiences a MAT of 8.16 ± 1.04 °C and receives an AP of 1228 ± 365 mm. Its characteristic indicator species were *Berberis darwinii*, *Azara microphylla*, and *Blechnum hastatum*. As a transitional type, it exhibits generally a lower number of diagnostic species and shares species with both the more humid communities (such as the broadleaved montane forests, with species like *Maytenus magellanica*, *Gaultheria phillyreifolia*, *Azara lanceolata* and *Raukaua laetevirens*; see Suppl. material 11) and the drier types (such as the coniferous forests, including the dominant species *Austocedrus chilensis*, *Lomatia hirsuta* and *Aristotelia chilensis*; see Suppl. material 11). The species richness (17.67 ± 5.91) and evenness (0.71 ± 0.1) in this community was higher than in the more humid or wetter types.

Coniferous montane forest (*Gavileo-Austrocedretum chilensis*). The mean annual temperature for this community is 8.18 ± 1.11 °C, with total annual precipitation averaging 992 ± 255 mm. It included 18 samples, spanning elevations from 500 to 1200 m a.s.l. This type displayed the highest species richness (26.68 ± 5.89) and evenness (0.77 ± 0.06) in the study area, illustrating a trend of increasing diversity from humid / hydric to dry / xeric conditions. These metrics highlight a vegetation unit characterized by

Table 1. Diagnostic species of the classified vegetation units displaying phi coefficient (Φ) only for significant indicator species (alpha > 0.01) and relative frequency across vegetation units (F) for all species. Large phi coefficients (Φ × 1000 > 300) are shaded in grey, with species arranged in descending order of phi within each vegetation type. Dots indicate species below the significance threshold for the vegetation unit, while dashes denote species with relative frequencies of zero.

	1. Broadleaved montane forest		2. Mixed montane forest		3. Coniferous montane forest		4. Woody subandean forest		5. Herbaceous subandean forest		6. Shrubland	
No. of relevés	**26**		**29**		**18**		**16**		**35**		**17**	
	Φ × 1000	**F**	**Φ × 1000**	**F**	**Φ × 1000**	**F**	**Φ × 1000**	**F**	**Φ × 1000**	**F**	**Φ × 1000**	**F**
Drimys andina	645	93	.	7	.	-	.	-	.	-	.	-
Berberis trigona	314	80	.	20	.	-	.	-	.	-	.	-
Desfontainia spinosa	255	100	.	-	.	-	.	-	.	-	.	-
Saxegothaea conspicua	255	100	.	-	.	-	.	-	.	-	.	-
Berberis darwinii	.	22	593	55	.	12	.	-	.	6	.	4
Azara microphylla	.	11	525	78	.	6	.	-	.	-	.	6
Blechnum hastatum	.	-	314	83	.	17	.	-	.	-	.	-
Acaena pinnatifida	.	-	.	-	806	73	.	-	.	18	.	9
Holcus lanatus	.	-	.	12	706	75	.	-	.	12	.	-
Arenaria serpyllifolia	.	-	.	-	674	100	.	-	.	-	.	-
Acaena splendens	.	-	.	-	650	90	.	-	.	10	.	-
Poa pratensis	.	-	.	-	583	80	.	-	.	20	.	-
Geranium magellanicum	.	5	.	23	578	55	.	-	.	9	.	9
Rumex acetosella	.	-	.	-	549	55	.	5	.	30	.	10
Carex patagonica	.	-	.	17	517	46	.	4	.	33	.	-
Balbisia gracilis	.	-	.	-	493	100	.	-	.	-	.	-
Collomia biflora	.	-	.	-	493	100	.	-	.	-	.	-
Eryngium paniculatum	.	-	.	-	485	86	.	-	.	-	.	14
Cirsium vulgare	.	-	.	-	439	100	.	-	.	-	.	-
Crepis capillaris	.	-	.	-	439	100	.	-	.	-	.	-
Trisetum caudulatum	.	-	.	-	439	100	.	-	.	-	.	-
Hypochaeris radicata	.	-	.	11	435	67	.	-	.	11	.	11
Dactylis glomerata	.	-	.	8	433	54	.	-	.	31	.	8
Solidago argentinensis	.	-	.	-	432	71	.	-	.	29	.	-
Colletia hystrix	.	-	.	22	431	67	.	-	.	-	.	11
Acaena argentea	.	14	.	14	418	71	.	-	.	-	.	-
Trifolium repens	.	12	.	-	399	62	.	-	.	25	.	-
Festuca myuros	.	-	.	-	378	100	.	-	.	-	.	-
Gavilea odoratissima	.	-	.	-	378	100	.	-	.	-	.	-
Koeleria permollis	.	-	.	-	378	100	.	-	.	-	.	-
Senecio filaginoides	.	-	.	-	378	100	.	-	.	-	.	-
Trifolium dubium	.	-	.	-	345	67	.	-	.	17	.	17
Aira caryophyllea	.	-	.	25	331	75	.	-	.	-	.	-
Baccharis racemosa	.	-	.	-	307	100	.	-	.	-	.	-
Bromus tectorum	.	-	.	-	307	100	.	-	.	-	.	-
Calceolaria sp	.	-	.	-	307	100	.	-	.	-	.	-
Madia sativa	.	-	.	-	307	100	.	-	.	-	.	-
Plantago lanceolata	.	-	.	-	307	100	.	-	.	-	.	-
Sisyrinchium patagonicum	.	-	.	-	307	100	.	-	.	-	.	-
Solidago chilensis	.	-	.	-	307	100	.	-	.	-	.	-
Veronica arvensis	.	-	.	-	307	100	.	-	.	-	.	-
Senecio subumbellatus	.	-	.	-	304	75	.	-	.	-	.	25
Fragaria chiloensis	.	8	.	17	299	42	.	-	.	25	.	8
Ribes densiflorum	.	9	.	-	.	-	662	52	.	39	.	-
Rubus geoides	.	-	.	-	.	-	655	75	.	25	.	-
Gaultheria pumila	.	-	.	-	.	-	554	78	.	11	.	11
Chiliotrichum diffusum	.	4	.	4	.	-	537	42	.	38	.	12
Empetrum rubrum	.	-	.	-	.	-	465	83	.	-	.	17
Perezia fonkii	.	-	.	-	.	-	433	80	.	20	.	-
Austrolycopodium magellanicum	.	25	.	-	.	-	427	62	.	12	.	-
Escallonia alpina	.	19	.	-	.	-	407	44	.	25	.	12
Senecio trifurcatus	.	-	.	-	.	-	402	100	.	-	.	-
Ourisia ruellioides	.	-	.	25	.	-	357	75	.	-	.	-
Misodendrum punctulatum	.	13	.	3	.	10	338	29	.	32	.	13
Senecio argyreus	.	-	.	-	.	14	334	57	.	14	.	14
Acaena magellanica	.	-	.	-	.	-	326	100	.	-	.	-
Poa sp	.	-	.	-	.	-	326	100	.	-	.	-
Lagenophora hariotii	.	20	.	-	.	-	285	40	.	30	.	10
Leucheria glacialis	.	-	.	7	.	-	.	-	565	93	.	-
Acaena ovalifolia	.	14	.	21	.	7	.	2	488	52	.	5

	1. Broadleaved montane forest		2. Mixed montane forest		3. Coniferous montane forest		4. Woody subandean forest		5. Herbaceous subandean forest		6. Shrubland	
No. of relevés	**26**		**29**		**18**		**16**		**35**		**17**	
	Φ × 1000	**F**	**Φ × 1000**	**F**	**Φ × 1000**	**F**	**Φ × 1000**	**F**	**Φ × 1000**	**F**	**Φ × 1000**	**F**
Galium fuegianum	.	12	.	6	.	6	.	-	414	75	.	-
Perezia prenanthoides	.	8	.	-	.	-	.	8	403	83	.	-
Calceolaria polyrrhiza	.	-	.	12	.	12	.	-	280	75	.	-
Nothofagus antarctica	.	-	.	8	.	20	.	-	.	8	769	64
Gaultheria mucronata	.	16	.	24	.	5	.	8	.	8	524	38
Azorella prolifera	.	-	.	-	.	14	.	-	.	-	506	86
Embothrium coccineum	.	17	.	28	.	10	.	-	.	10	401	34
Senecio bracteolatus	.	-	.	-	.	-	.	-	.	-	389	100
Baccharis elaeoides	.	-	.	-	.	-	.	-	.	-	316	100
Discaria chacaye	.	-	.	-	.	-	.	-	.	-	316	100
Diostea juncea	.	-	.	12	.	25	.	-	.	12	296	50

high diversity and low dominance of competitive species. However, a high proportion of non-native species (5.32 ± 3.04; Figure 5) composes this community. It also included light-demanding and drought-adapted native species with a distribution extending into the steppe, such as *Balbisia gracilis*, *Eryngium paniculatum*, *Collomia biflora*, *Acaena splendens*, *Acaena pinnatifida*, *Solidago chilensis*, *Viola maculata* and many grass species. Additionally, resprouting shrubland species characteristic also of the shrublands, were common in this assemblage, including *Schinus patagonica*, *Maytenus boaria*, and *Maytenus chubutensis*.

Woody subandean forest (*Macrachaenio-Nothofagetum pumilionis*). This is a humid subandean community occurring at the western and uppermost elevations of our study area. We covered 16 plots within this community, which ranged from 1200 to 1600 m a.s.l. The community experiences a MAT of 5.1 ± 0.67 °C and receives an average annual precipitation of 1080 ± 168 mm. Positioned near the treeline, this community typically has overstories of *Nothofagus pumilio*, which can also take on a dwarf form under these conditions. Fifteen species are diagnostic species of this type, including *Escallonia alpina*, *Ribes densiflorum*,

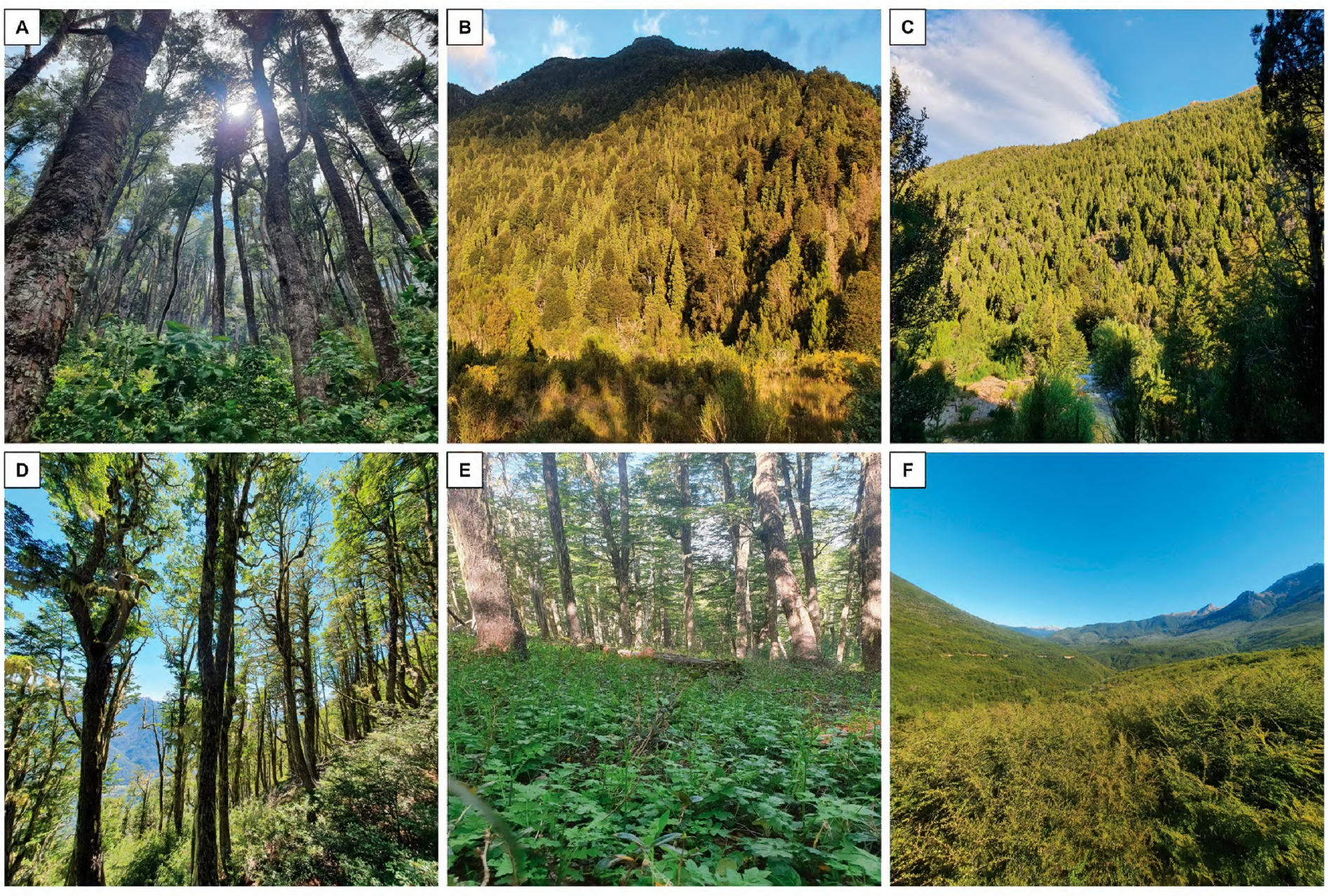

Figure 4. Illustrative photographs of the classified vegetation units: **A)** Broadleaved montane forest (*Myrceugenio-Nothofagetum dombeyi* Esk. 1968); **B)** Mixed montane forest (*Austrocedro-Nothofagetum dombeyi* Esk. 1968); **C)** Coniferous montane forest (*Gavileo-Austrocedretum chilensis* Esk. 1968); **D)** Woody subandean forest (*Macrachaenio-Nothofagetum pumilionis* Esk. 1973); **E)** Herbaceous subandean forest (*Anemono antucensis-Nothofagetum pumilionis* Oberd. 1960); **F)** Shrublands (*Lomatio hirsutae-Nothofagetum antarticae* Esk. 1969). Credit: Natalia Joelson.

Chiliotrichum diffusum, *Lagenophora hariotii*, *Austrolycopodium magellanicum*, and *Rubus geoides* are tolerant to snow and cold. The mean species richness was 12.92 ± 4.52 and Pielou's Evenness was 0.59 ± 0.18, indicating low diversity and dominance of competitive species, similar to the broadleaved humid forests in the montane belt.

Herbaceous subandean forest (*Anemono antucensis-Nothofagetum pumilionis*). This community was found in the drier eastern subandean portions of the study area. It comprised 35 samples in our study and it was located at elevations ranging from 1100 to 1600 m a.s.l. These herb-rich understories have diagnostic species such as *Leucheria glacialis*, *Acaena ovalifolia*, and *Perezia prenanthoides*, the latter being a characteristic species shared by both subandean vegetation types. Other species like *Berberis serrato-dentata*, *Adenocaulon chilense*, *Chusquea culeou*, *Maytenus disticha*, and *Macrachaenium gracile*, can tolerate warmer conditions and were found in both woody subandean forests and the broadleaved montane forests. This community also harbors a variety of generalist species often designated as companion taxa, such as *Alstroemeria aurea*, *Myoschilos oblongum*, *Osmorrhiza berteroi*, *Ribes magellanicum*, and *Austroblechnum penna-marina*. The average species richness per plot is 12 ± 3 and Pielou's Evenness is 0.7 ±0.13, showing greater diversity and evenness compared to the humid subandean type. The MAT here is 5.62 ± 0.54 °C, with annual precipitation averaging 842 ± 127 mm.

Shrubland (*Lomatio hirsutae-Nothofagetum antarticae*). We surveyed 17 plots in this community, primarily dominated by resprouting species and situated at elevations from 900 to 1400 m a.s.l. *Nothofagus antarctica*, often taking a dwarf form, is a typical dominant species. The community has an average annual temperature of 6.45 ± 0.86 °C and receives about 898 ± 145 mm of rainfall annually. It typically occurs on north-facing slopes, which receive more solar radiation, in the drier eastern areas or on exposed mid-slopes. It had a mean species richness of 17.11 ± 6.49 and an evenness of 0.63 ±0.15. It is characterized by the dominance of resprouting species, with high fidelity observed in species such as *Gaultheria mucronata*, *Diostea juncea*, and *Embothrium coccineum*. Additionally, some species were diagnostic of coniferous forests, including *Berberis microphylla*, *Ribes cucculatum*, *Baccharis* spp., *Mutisia* spp., *Fabiana imbricata*, and *Discaria articulata*.

General patterns along the environmental gradients

The unconstrained ordination (NMDS) with three dimensions had a stress value of 0.14. The six vegetation units were clearly distinguishable in the three-dimensional space. The first axis, which represents the strongest gradient, correlates highly with elevation (see Figure 5 and Suppl. material 9). Along this axis, vegetation types displayed clear differentiation based on temperature preferences: mixed montane and coniferous montane forests occupied the warmer, lower elevation range, followed by shrublands and broadleaved montane forests in intermediate conditions, with subandean forests situated at higher, and colder elevations. In this dimension, both coniferous forests and shrublands show relatively young stands, high species richness, and a high number of non-native species.

The second axis was primarily associated with annual precipitation (AP) and basal area. Coniferous forests and

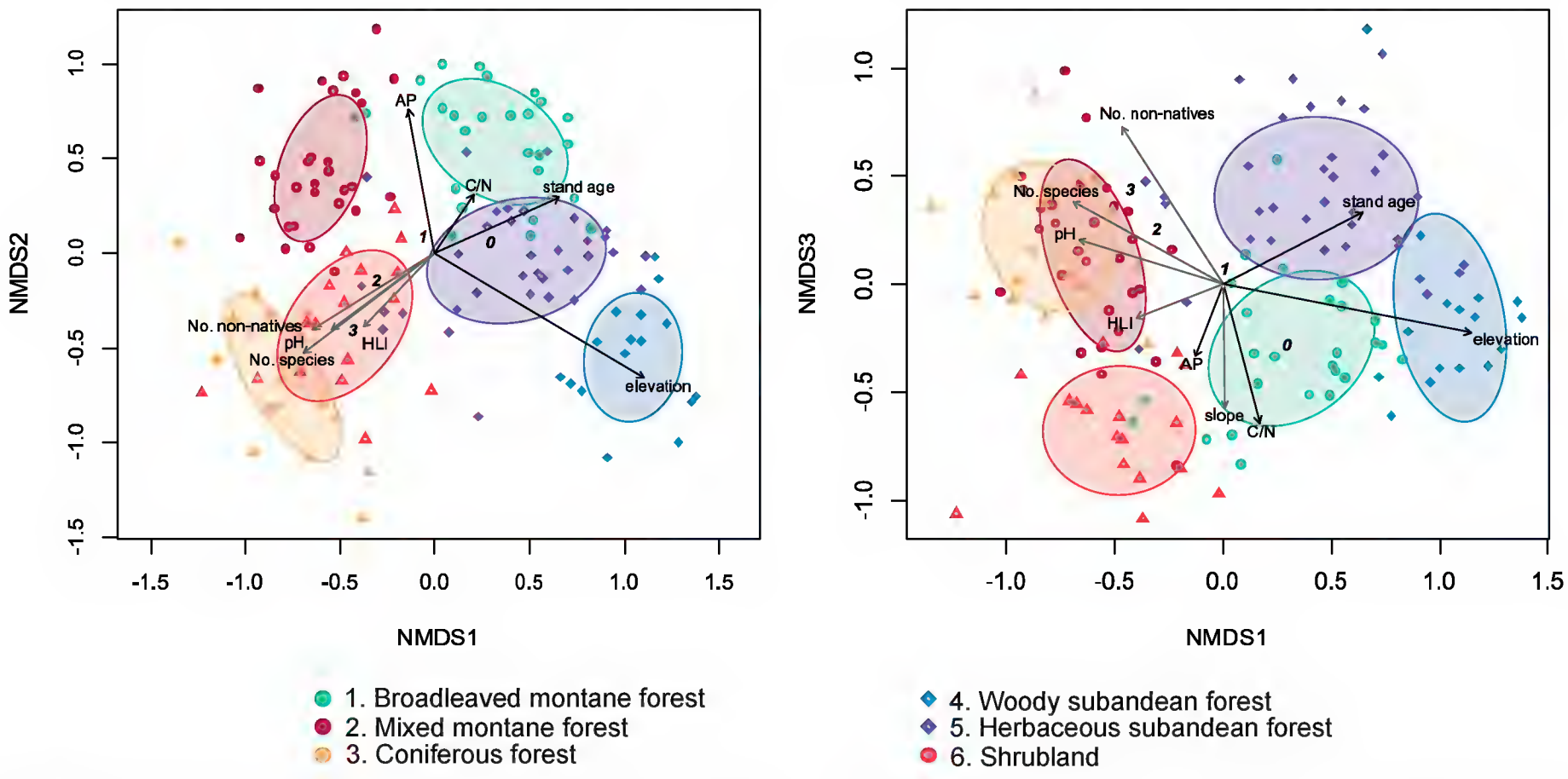

Figure 5. NMDS ordination diagrams with 141 sites (stress 0.14). Sites are colored by vegetation types. The ellipses express standard deviations of points within each type at the 0.5-level. Suppl. variables were added post-hoc to the diagrams with only significant variables for the respective axis combination shown ($p < 0.05$, see Suppl. material 9: table S.9.2). Variables which had a significant effect in the db-RDA (Suppl. material 9: table S.9.1) are printed in **black**, the remaining ones in grey. The factor levels represent the browsing index categories are 0 = no use, 1 = low use, 2 = moderate use, 3 = high use.

shrublands were positioned at the drier end, while subandean forests occupied intermediate moisture levels, and broadleaved to mixed montane forests were located at the wettest end. The third axis primarily captured variations in the C/N ratio, with shrublands showing low N soils. Furthermore, the browsing index, mostly indicating the degree of grazing use, increased towards the drier communities. While shrublands and broadleaved montane forests were differentiated along the second axis by precipitation and stand age, they showed no significant differences along the third axis concerning nitrogen availability.

Soil characteristics

We found differences across the types regarding their soil properties (Figure 6), in both C/N ratios (Kruskal-Wallis test, $\chi^2_5 = 38.7$, $p < 0.001$) and pH values (Welch ANOVA, $F_{5, 56.3} = 12.3$, $p < 0.001$). Overall, we found a moderate correlation between the C/N ratios of the humus and mineral soil layers ($r = 0.44$). The variation in pH value reflected the species richness gradient, increasing towards drier conditions and lower elevations. In contrast, C/N ratios displayed an inverse trend, being lowest at lower elevations and within the driest community (coniferous montane forest). The shrubland community showed a large dispersion in its C/N ratios and the mixed montane forest community a large dispersion in its pH values. The most significant pH differences were observed along the moisture gradient rather than elevation, with the largest differences between drier (coniferous forests and shrublands) and more humid communities (Figure 6C). This pattern was less pronounced when comparing montane to subandean types. While C/N ratios also varied, these differences were generally less pronounced and more responsive to precipitation gradients, particularly at higher elevations. Here, woody subandean forests demonstrated higher C/N ratios compared to herbaceous subandean forests (Figure 6D).

Forest structure and land-use patterns

The predominant canopy species of the broadleaved and mixed montane forests is *Nothofagus dombeyi*, with drier forests having a more diverse tree composition, including *Austrocedrus chilensis*, *Lomatia hirsuta*, *Maytenus boaria* and *Nothofagus pumilio* in higher areas. The basal area in the subandean types is contributed entirely by *Nothofagus pumilio*, and primarily by *Nothofagus antarctica* in shrublands. The coniferous forest was the most diverse in their overstory species, with the largest contribution from *Austrocedrus chilensis* (Figure 6F). Basal area is lowest in shrublands with 10 m^2 per ha, increasing to approximately 50 m^2 per ha in mixed and broadleaved montane forests and herbaceous subandean forests, while it showed intermediate values in coniferous forest and woody subandean forests (Suppl. material 10).

The shrublands represents the youngest community, followed by the coniferous forest and mixed montane forests, as indicated in Figure 6E. The oldest communities are broadleaved montane and herbaceous subandean forests, averaging over 200 years. There is a clear negative

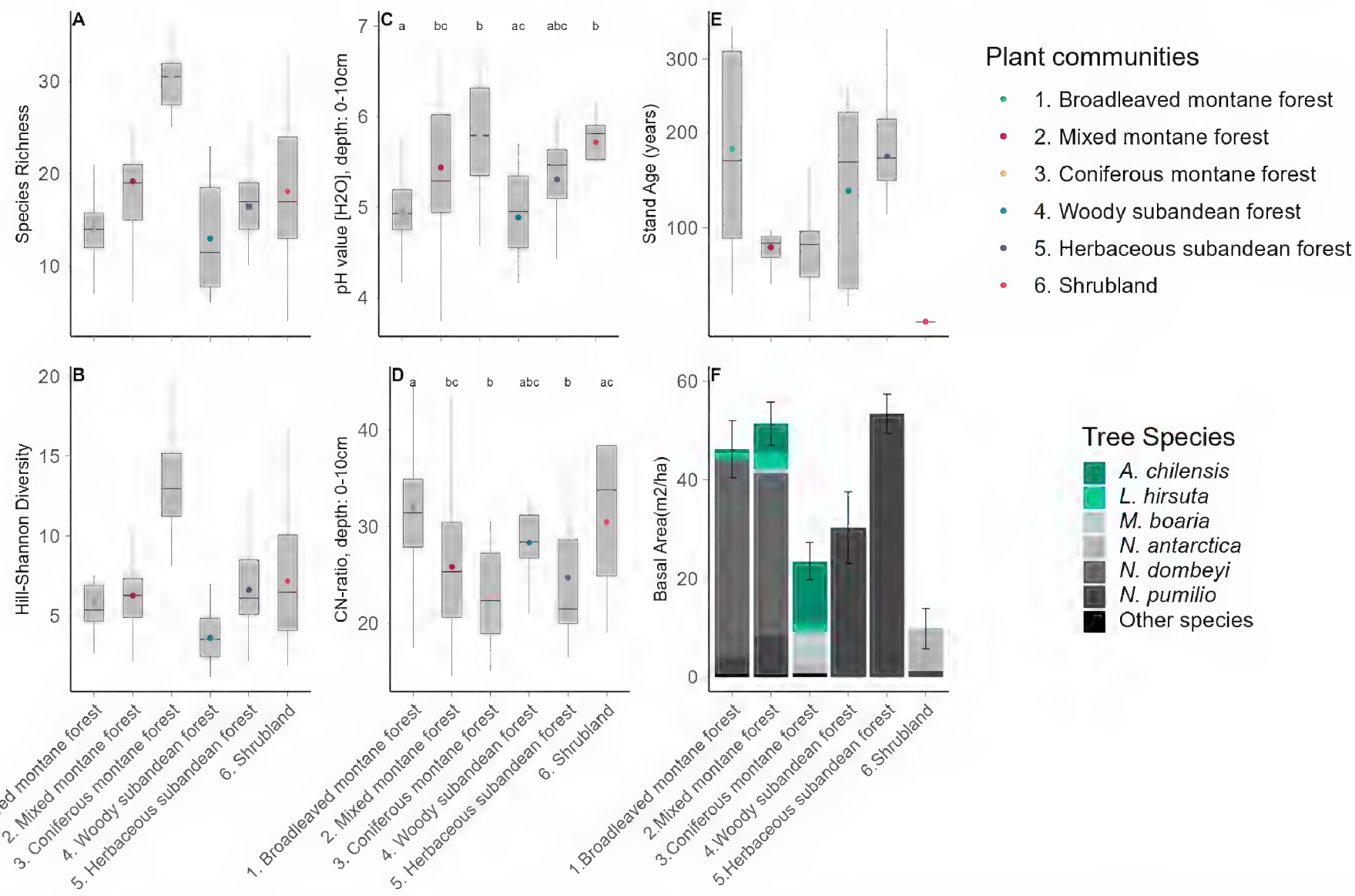

Figure 6. Diversity, soil and forest structure metrics across the six vegetation units. The means are colored by vegetation unit. Panels (**A**) through (**D**) (**A.** Species Richness, **B.** Hill-Shannon Diversity, **C.** Soil pH value, and **D.** Soil C/N ratio) are based on a sample size of n = 141. Panels (**E**) and (**F**) (**E.** Stand Age and **F.** Basal Area) are derived from field biometric plots with a sample size of n = 66. Stand Age y-axis is squared-root scaled.

correlation between stem density and stand age (r = -0.61), whereas older forests tend to have a higher basal area (r = 0.34). The younger mixed montane forests, due to the participation of *Nothofagus dombeyi*, have a basal area as large as the oldest communities do, although the similarly aged coniferous forest have a significantly lower value due to its lower stem density.

Browsing intensity differed among communities, being particularly high in the coniferous forest, as indicated by the high proportion of non-native and pasture species. In contrast, the mixed montane forests and shrublands experience moderate browsing, while the subandean and broadleaved montane communities experience low to no browsing. A significant relationship was found between browsing intensity and logging activities, with higher browsing associated with increased logging (Fisher's exact test, $p < 0.001$). The diversity metrics for the coniferous forest type revealed a vegetation unit characterized by high diversity and a low dominance of competitive species. However, this diversity includes a significant proportion of non-native (20.4 ± 11.7%; Suppl. material 11) and/or light-demanding species, many of which are diagnostic for this type, such as *Holcus lanatus*, *Arenaria serpyllifolia*, *Geranium molle*, *Hieracium patagonicum*, *Rosa rubiginosa*, *Hypochaeris radicata*, *Solidago chilensis*, *Rumex acetosella*, and *Dactylis glomerata*.

Discussion

Effects of environment on species composition and diversity

Our study provides new insights into vegetation distribution patterns under varying environmental conditions in the temperate Andean forests and shrublands of NW Patagonia. Elevation emerged as the strongest predictor of community composition, reflecting a crucial role of temperature —a well-established driver of vegetation distribution (Woodward 1987). We observed a significant and steep turnover in species composition along the elevation gradient, which remained consistent across different moisture regimes. The plant communities were also well differentiated along the precipitation and soil chemical gradients. Besides climatic effects, we found a significant association of browsing, forest age, and tree basal area with species composition. Non-native species were predominantly found in young stands with high human influence, whereas evergreen hygrophyllous shrubs were more abundant in older forests with less human and livestock influence.

We found differences in the predictor value of the variables. While precipitation was the second-best predictor, its influence on species composition was considerably less than that of elevation. However, it is widely recognized that precipitation alone does not accurately represent moisture availability, which is also significantly influenced by atmospheric saturation deficit, soil characteristics, and topography—factors such as slope direction and shape, as well as the high water retention capacity of Andosol soils, which can make water available to vegetation during the dry summer months (Buduba et al. 2020). In line with existing research (Huertas Herrera et al. 2018; Rosas et al. 2024), lower-elevation communities showed more non-native species. This pattern has been explained previously by shorter distances to settlements and infrastructure, higher intensities of land-use and human-caused disturbances, easier access for humans and livestock, and more available ecological niches (Speziale and Ezcurra 2011). The strong relationship between stand age and species composition also highlights the importance of succession in shaping vegetation patterns (Kitzberger 2012; Kitzberger et al. 2022).

We also found that land-use activities, represented by browsing intensity and associated logging, have a significant impact on vegetation composition. Our findings match existing literature that showed browsing to reduce woody vegetation, encouraging the growth of herbaceous plants and introducing species typically found in pastures (de Paz and Raffaele 2015; Piazza et al. 2016; Soler et al. 2022). Both grazing and logging practices tend to increase alpha-diversity and reduce beta-diversity, promoting non-native species and leading to vegetation homogenization (Soler et al. 2019; Chillo et al. 2020). Furthermore, the clonal and ruderal species identified as characterizing open areas in coniferous forest and shrublands match those found by other studies assessing post-disturbance colonization in clear-felled sidehills (Puntieri 1991). These results present a concerning future scenario, as previous studies in Patagonia have highlighted the synergistic effects of browsing and fire disturbance. Plant traits that allow persistence under pressure from introduced herbivores also increase flammability, thus favoring species persistence following recurrent fires (Blackhall et al. 2008; Veblen et al. 2011).

The patterns of plant diversity along bioclimatic gradients are consistent with those reported in previous literature (McCain and Grytnes 2010). A clear pattern is observed showing diversity to decrease toward higher elevations, likely due to thermal species filtering. Although some studies indicate that a complex interaction between water and energy shapes biodiversity along elevation gradients rather than the dominance of a single factor (Vetaas et al. 2019), our current study is unable to unravel these relationships. In forest types characterized by high humidity, species richness and evenness tend to be lower, suggesting that a few competitive species dominate, leading to less diverse plant communities on a smaller, plot-sized scale. On these sites, tree productivity is higher and over the years, canopy cover (indirectly measured by basal area; Mitchell and Popovich 1997) increases, reducing light availability on the forest floor. Moreover, certain species like *Drimys andina*, *Chusquea culeou*, and *Gaultheria phillyreifolia* often create dense thickets that are low in height and cover large areas. This suggests that higher precipitation and humidity indirectly influence herb layer species richness by promoting the trees in the canopy layer, which suppress the understory through asymmetric

competition. Conversely, drier conditions are associated with more diverse communities that are richer in species and more even. However, these areas also tend to experience more frequent fires, as indicated by younger forests and greater impacts from browsing animals. The multidimensional factors that explain the observed patterns, can therefore not be considered in isolation, but as an interlinked set of factors.

Soil chemistry, particularly pH values and, to a lesser extent, the C/N ratio, showed significant variation across our study region and closely correlated with vegetation types. In apparent contrast, shrublands can develop in a wide range of site conditions, as observed by Seibert (1979) and Eskuche (1973). There is a wealth of literature showing that soil chemistry influences the species composition of forests and their herbaceous layers (e.g., (Gilliam 2014; Leuschner and Ellenberg 2017), but also of vegetation feedbacks on the soil, when plants influence soil chemistry through the chemical composition of their litter (e.g., Alauzis et al. 2004; Cools et al. 2014). We found C/N ratios to be higher in moister and colder areas, corresponding to broadleaved and subandean forest types. This is primarily due to slower N turnover in colder environments and humid habitat life forms producing more recalcitrant litter, leading to lower relative potential net N mineralization rates (Bertiller et al. 1995). These results also match previous findings on most species of the wet forest being proficient for nitrogen (Satti et al. 2007; Diehl et al. 2008). In parallel, pH values decreased from drier to wetter and from warmer to colder communities, associated with a decrease in plot-level plant diversity, which is a consequence of enhanced leaching of basic cations in more humid environments. This decreasing tendency can also be explained by fire disturbance being more frequent in drier areas and increasing soil pH (Alauzis et al. 2004). The highest pH found in coniferous forests can also be explained by the high dominance of *Austrocedrus chilensis* and the high calcium content in its senescent leaves (Mazzarino and Gobbi 2005). Our pH values correspond to those detected by Eskuche (1999), who also noted increasing values from humid (6 to 5.1) to dry vegetation types (6–6.4), though with less pronounced differences.

The relationship between soil acidity and plant species richness has been investigated both at the biome level (Azevedo et al. 2013; Crespo-Mendes et al. 2019) and at the local scale (e.g., Crawley et al. 2005; Pärtel et al. 2004; Stevens et al. 2010). According to the species pool hypothesis (Pärtel 2002), plant diversity at the regional scale is influenced by the soil conditions in which the species originally evolved, leading to either positive or negative relationships between diversity and soil pH. Our results indicate a positive relationship between soil pH and species richness for the NWPatagonian forest region. Moreover, the data suggest that soil chemical properties are a key predictor of plant community composition in this region—an aspect that has been overlooked in the past (Pollmann 2001)—and should be a critical area for further ecological research and conservation planning.

Identification and diagnosis of plant communities

We catalogued 241 vascular plant species from 70 families, arranging them into six plausible plant communities. Each community presents a distinct composition and thrives in different thermal, hydric, and soil chemical conditions (Suppl. material 10). When compared to the traditional syntaxa described by Eskuche (1999), Pollmann (2001) and Amigo and Rodríguez-Guitián (2011, 2015), our analogous communities align well with their bioclimatic diagnoses, but exhibit some floristic differences. Overall, we found many species being diagnostic of more than one type, or generalist species present in multiple types, which is less observed in traditional classifications (Suppl. material 11). This results from our use of systematic sampling and numerical analytical methods, whereas early phytosociologists focused on distinguishing between "climax associations", excluding transitional successional states (Eskuche 1973).

Our results show a greater match in diagnostic species of expert-based defined types in the humid than in the drier areas. This may be due to higher land use and conversion rates in these ecotonal areas (Kitzberger 2012). Species characteristic of wetter types, such as *Gaultheria phillyreaefolia*, *Drimys andina*, and *Azara lanceolata*, are consistently present in both historical and current relevés. This does not occur in the mixed forests (comparable to *Austrocedro-Nothofagetum dombeyi*) or coniferous forest (comparable to *Gavileo-Austrocedretum chilensis*) types, where the species named in historical records seem to be generalists and with less diagnostic value in our current study. This discrepancy is also evident in the subandean vegetation types *Anemono antucensis-Nothofagetum pumilionis* Oberd. 1960 and *Macrachaenio-Nothofagetum pumilionis* Esk. 1973. These types match very well the bioclimatic diagnosis of the herbaceous and woody subandean types, respectively. Amigo and Rodríguez Guitián (2015) and (Hildebrand-Vogel et al. 1990) interpret the *Anemono antucensis-Nothofagetum pumilionis* as having a drier sub-Mediterranean bioclimatic character, in the contact zone to the Mediterranean bioclimate, which influences the floristic differences between these subandean forests and those with wetter climate influences. *Macrachaenio-Nothofagetum pumilionis* is characteristic of Argentinian lenga forests with wetter climate influence and includes species typical of upper forest edges, such as *Senecio argyreus* and *Chiliotrichum diffusum*. However, the units found in our current study present some floristic differences from the traditional types. From the characteristic species set of this unit—*Anemone antucensis*, *Valeriana laxiflora*, *Vicia nigricans*, *Alstroemeria aurea*, and *Leucheria glacialis*—only the latter was diagnostic of the herbaceous subandean forests in our study, while *Anemone antucensis* was absent in our study area and the rest of the species showed a more generalistic behavior. Conversely, the woody type retains many species named for the *Macrachaenio-Nothofagetum pumilionis* unit or for *Anemono antucensis-Nothofagetum pumilionis* with low human influence (e.g., *Chiliotrichum diffusum*, *Escallonia alpina*, *Austrolycopodium magellanicum*, *Senecio* spp., *Carex* spp.; Amigo and Rodríguez Guitián 2015)

Findings from Eskuche (1968) support the idea that grazing is the main driver of composition change, identifying species such as *Diplolepis descolei*, *Loasa* spp., and *Gavilea glandulifera* as diagnostic for unaltered forests, all of which were rare in our study area. Seibert (1979) also highlighted the association of the *Gavileo-Austrocedretum-chilensis* community with high browsing intensity. He pointed out that these drier forests are heavily impacted by fire and grazing, leading to the regression of understory species and the proliferation of weeds and European pasture species, similar to those patterns noted in the coniferous forest. While land use plays an important role, we believe that sampling and classification bias also influences this result. Thus, traditional classifications being mostly carried out in Chilean forests result in a better match for western wetter Argentinian forests.

At the association level, the indicator species provided by (Eskuche 1999) largely align with our findings. However, the reclassifications proposed at higher hierarchical levels do not match the numerical classification. Although Pollmann's classifications (based on a larger regional scale and from a northern region not overlapping with our study) seem to be more applicable to our area, as Pollmann (2001) pointed out, we observed a significant split and differentiation of species between the *Nothofagetea pumilionis-artarcticae* (subandean forests) and *Wintero-Nothofagetea* (evergreen forests and shrublands). This differentiation explains the high species turnover along the elevation gradient, which is much more pronounced than along the precipitation gradient and aligns better the biogeographic classifications for the region (Cabrera 1976; Morrone 2001).

Some identification issues already partially addressed by Amigo and Rodríguez-Guitián (2011, 2015) might have led to the reclassification proposed by Eskuche (1999). Several species cited as diagnostic for the *Nothofagetea pumilionis-artarcticae* class, such as *Maytenus disticha*, *Ovidia andina*, and *Carex* spp., pose determination problems and led to placing the Argentinian *Nothofagus* forests in the mentioned class. Moreover, many species cited as characteristic for the class *Nothofagetea* and order *Berberido-Nothofagetalia antarcticae* are accompanying species cited by Pollmann (2001) (generalist species *Vicia nigricans* and *Alstroemeria aurea*). This suggests a local bias in classifications affected by different ecological conditions. In our interpretation, these biases mainly arise from considering a truncated moisture gradient, shaped by the rain shadow effect of the Andes, due to administrative borders: in Chile, forests are structured predominantly by climate, while in Argentina, they are influenced by both climate and fire disturbance. This issue calls for more comprehensive sampling in Argentinian sub-Mediterranean areas and a broader classification system that incorporates this data.

Conclusion

The environmental control on plant species composition and diversity evidenced by our study highlights opportunities for targeted management in scenarios concerning climate change. Human influence, as characterized by the land-use indicators of grazing and logging in our study, significantly affects plant community composition. Additionally, basal area and stem density (negatively correlated to stand age) of the tree layer significantly influence biodiversity, suggesting that forest management should aim to preserve optimal density ranges for each forest type to enhance conservation efforts (Forrester and Bauhus 2016; Hedwall et al. 2019). However, further research is needed to explore this relationship.

The strong link between climate factors—notably temperature and precipitation—and vegetation patterns emphasizes the pivotal role of climate in shaping these communities. Current scenarios of rising temperatures and increasing drought imply increased risks of wildfires, amplified by vegetation shifts from high forests to more flammable, pyrophilous shrublands (Kitzberger et al. 2022). Similarly, non-native species often thrive in disturbed sites (Jauni et al. 2015). The potential risk of biotic exchange due to the invasion of non-native species from neighboring pastures and exotic pine plantations thus poses a significant threat to the remaining phytodiversity of native plant communities and their replacement by novel communities.

Our analysis has led to the initial statistical clustering of plant communities and the identification of key environmental characteristics and indicator species for the study area. Identifying diagnostic and indicator species for each plant community offers valuable ecological insights and tools for future monitoring and surveillance. These species, which are highly adapted to specific environmental conditions, can be used to track ecological changes and inform restoration efforts. On both regional and local scales, our results lay an evidence-based groundwork for management, monitoring, and conservation planning.

Data availability

The data and code for this study are available at https://doi.org/10.5281/zenodo.14206361.

Author Contributions

Conceptualization: NJ, HW, SZ; Data collection: NJ, AS, GL; Formal analysis: NJ; FvL; Funding acquisition: HW, SZ; Investigation: NJ; Methodology: NJ, FvL; Visualization: NJ, AS; Writing, original draft preparation: NJ, Writing - review & editing: all authors.

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Supplementary material

Supplementary material 1
Map of areas presenting moderate to high burn severity between 1984 and 2023 (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl1

Supplementary material 2
List of topographic, bioclimatic, forest structure, soil, and land use predictor variables included in the models (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl2

Supplementary material 3
Description of browsing and logging index categories (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl3

Supplementary material 4
Statistical analysis for determining appropriate cutting levels for vegetation clustering (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl4

Supplementary material 5
List of species employed in the assignment of clusters to syntaxonomic units (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl5

Supplementary material 6
Summary of meteorological data of El Bolsón Weather Station and calculations for bioclimatic diagnosis (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl6

Supplementary material 7
List of species recorded in the study area (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl7

Supplementary material 8
Floristic summary of life forms and taxonomic groups in the study area (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl8

Supplementary material 9
Statistical results of the db-RDA and post-hoc correlation of supplementary variables onto the NMDS (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl9

Supplementary material 10
Bioclimatic classification and summary of mean predictor values and diversity indices of the vegetation units (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl10

Supplementary material 11
Table of indicator species for more than one cluster (pdf).
Link: https://doi.org/10.3897/VCS.134621.suppl11

Supplementary material 12
Ordered relevé table of the broadleaved and coniferous montane forests (csv).
Link: https://doi.org/10.3897/VCS.134621.suppl12

Supplementary material 13
Ordered relevé table of the woody and herbaceous subandean forests (csv).
Link: https://doi.org/10.3897/VCS.134621.suppl13

Supplementary material 14
Ordered relevé table of the shrublands (csv).
Link: https://doi.org/10.3897/VCS.134621.suppl14